On the Inheritance of Eye-colour in Man.

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(Communicated by W. Bateson, F.R.S. Received May 7,—Read November 14, 1907.)

The following notes on the inheritance of eye-colour in man are based on material examined by the writer in the village of Burbage, Leicestershire. During the past three years, 139 pairs of parents and 683 of their offspring have been examined, with the following results:—

Eye-colour in man depends almost wholly on the colour of the iris. The colour of the iris varies considerably in different families and often in different individuals of the same family. This variability is due partly to the presence or absence of different pigments on the anterior and posterior surfaces of the iris, and partly, in all probability, to actual differences in the structure of the iris.

In the Report of the Anthropometric Committee of the British Association for 1880, the following statement concerning the nature of eye-colour in man is given by Mr. Charles Roberts (pp. 134 to 136):—

"The iris, on which the colour of the eye depends, is a thin membranous structure, composed of unstriped muscular fibres, nerves, and blood-vessels, held together by a delicate network of fibrous tissue. On the inner surface of this membrane there is a layer of dark purple pigment called the *uvea* . . . and in brown eyes there is an additional layer of yellow (and, perhaps, brown-red) pigment on its outer surface also, and in some instances there is a deposit of pigment amongst the fibrous structures. In the albino where the pigment is entirely absent from both surfaces of the iris, the bright red blood is seen through the semi-transparent fibrous tissues of a *pink* colour; and in blue eyes, where the outer layer of pigment is wanting, the various shades are due to the dark inner layer of pigment—the *uvea*—showing through fibrous structures of different densities or degrees of opacity.

"The eyes of new-born infants . . . are dark blue, in consequence of the greater delicacy and transparency of the fibrous portion of the iris; and as these tissues become thickened by use, and by advancing age, the lighter shades of blue and, finally, grey are produced, the grey, indeed, being chiefly due to the colour of the fibrous tissues themselves. In grey eyes, moreover, we see the first appearance of the superficial layer of yellow pigment in the

form of isolated patches situated around the margin of the pupil, or in rays running across the iris.

"In the various shades of green eyes the yellow pigment is more uniformly diffused over the surface of the iris, and the green colour is due to the blending of the superficial yellow pigment with the blue and grey of the deeper structures. In the hazel and brown eyes the *uvea* and the fibrous tissues are hidden by increasing deposits of yellow and brown pigment on the anterior surface of the iris, and when this is very dense, black eyes are the result."

The above statement agrees well with my own observations, though I would add that the presence of the superficial layer of yellow pigment, when only slightly developed, is to be seen in blue eyes as well as in grey eyes.

No albinos were met with in the material examined by me, and my observations, therefore, relate to pigmented eyes only.

It has generally been supposed that the various types of eye-colours grade into each other without sensible breaks of continuity. A critical examination, however, shows that there is a distinct discontinuity between:—

(1) The eyes in which two kinds of pigments are present; the one, yellow-brown in colour, deposited on the outer or anterior surface of the iris; the other, blue-black in colour, deposited on the inner or posterior surface of the iris. Such eyes I propose to call *duplex*.

(2) The eyes in which the posterior pigment alone is present in the iris, the anterior pigment being absent. Such eyes may be called *simplex*. The application of popular names to these types is uncertain and quite unreliable; but, in general, eyes that would be called brown belong to the duplex type, while many of the blues and some of the greys belong to the simplex type.

(1) *The Duplex Type.*

To the duplex type belong the various shades of eyes with both anterior and posterior pigments.

In my observations, three distinct patterns of duplex eyes were found, viz.:—

(*a*) The *self-coloured* duplex, in which the anterior pigment is distributed over the whole front of the iris, practically obscuring the posterior pigment as in ordinary brown eyes.

(*b*) The *ringed* duplex, in which the anterior pigment is confined to a ringed area round the pupil, leaving the ground colour of posterior pigment clearly exposed round the periphery of the iris.

(*c*) The *spotted* duplex, in which the anterior pigment is broken up into distinct blotches or spots irregularly scattered over the posterior pigment which forms the ground colour.

Self-coloured duplex eyes vary in shade, presenting different grades of anterior pigmentation. In the darker brown shades the anterior pigment is more densely deposited than in the lighter green shades, the green effect being produced by a thin layer—or in some cases merely a fine irroration—of yellow pigment above the blue posterior layer.

Ringed duplex eyes similarly vary in shade, presenting different grades of anterior pigmentation. In my experience, the distribution of anterior pigment is always denser immediately round the pupil, both in self-coloured and ringed duplex eyes. Eyes with a ring of anterior pigment round the periphery of the iris, but without anterior pigment round the pupil, were not found in my observations.

Spotted duplex eyes also present different grades of anterior pigmentation. The pigmented areas also vary in size and number in different individuals and in the two eyes of the same individual.

Low-grade forms of the ringed duplex pattern are apparently numerous: under ordinary observation these might no doubt pass as blue or grey simplex eyes, the small pigmented ring so blending with the dark pupil as to be unrecognised at a short distance.

Similarly, low-grade forms of the spotted duplex pattern would also pass as blue or grey simplex eyes at a short distance. In both cases, however, a closer inspection reveals their true nature.

In carrying out my observations, I found that about half of the eyes, which appeared to be simplex when viewed in the ordinary way, were really duplex when closely examined in a good light.

Eyes presenting grades of anterior pigmentation so low that they can be mistaken for simplices have not occurred in my experience, and if such eyes do occur, they must be extremely rare in the population which I have studied.

In duplex eyes the anterior pigment is visible soon after birth, so that quite young infants are included in my observations. That anterior pigmentation tends to increase with age in young children is evident from the results of my observations during three years, though to what extent is not yet clear, owing to the limited period of observation.

(2) *The Simplex Type.*

To the simplex type belong the various shades of eyes with posterior pigment only, the anterior pigment being quite absent, as in all clear blue and clear grey eyes.

The darker shades of blue are apparently due to the greater delicacy and transparency of the fibrous tissues of the iris through which the posterior

pigment is seen, while the lighter shades of blue and the coarser greys seem to be due to the greater coarseness and opacity of the same tissues.

These structural differences appear to be continuous, a series of intermediate blue-greys linking up the finer blues with the coarser greys.

A further complication arises from the fact that, in most cases, the finer tissues of the iris become coarser with age, and young children with dark blue eyes may mature into adults with light blue, blue-grey, or grey eyes.

I have found striking illustrations of this in large families, where a whole series of shades from blue to grey were seen, the younger children being blue and the older ones grey. Consequently, no attempt has been made to distinguish between the many shades of clear blue and clear grey eyes, but all eyes with posterior pigment only are classed as simplex.

Finally, the clear blue and clear grey simplex eyes, with no trace of anterior pigment, must be carefully distinguished from the numerous low-grade duplex eyes, previously noted, which are often called "blue" or "grey."

Heredity of the Duplex and Simplex Types.

All families with less than two children are omitted, and families of two were not taken freely. At first, the largest families available were selected, but afterwards it seemed desirable to study collaterals, consequently some small families are included.

Out of the 139 families observed, 20 were simplex matings, 50 were duplex matings, and 69 were duplex-simplex matings.

Simplex Matings.

The 20 matings of simplex females with simplex males produced 101 offspring, all of the simplex type. Table I gives the numbers found in each family. Each family is distinguished by the number and initials of the male parent:—

Table I.—Simplex × Simplex.

Number and initials of ♂ parent.	Duplex.	Simplex.	Total offspring.
15 A. F.	0	4	4
27 J. T.	0	12	12
31 D. N.	0	11	11
89 J. M.	0	3	3
91 S. H.	0	3	3
93 F. G.	0	12	12
97 H. C.	0	6	6
101 J. L.	0	7	7
105 T. S.	0	4	4
113 E. D.	0	2	2
133 W. D.	0	4	4
137 J. C.	0	7	7
217 J. A.	0	4	4
221 J. D.	0	2	2
231 W. K.	0	5	5
235 A. B.	0	7	7
243 J. F.	0	2	2
255 J. H.	0	2	2
257 J. C.	0	2	2
277 A. A.	0	2	2
20	0	101	101

Duplex Matings.

The 50 matings of duplex females with duplex males gave two kinds of results: (*a*) 37 families produced 195 offspring, all of the duplex type; (*b*) 13 families produced 63 offspring, of which 45 were duplex and 18 simplex. Tables II (*a*) and (*b*) give the numbers found in each family.

Table II.—Duplex × Duplex.

No. and initials of ♂ parent.	Duplex.	Simplex.	Total offspring.
(*a*) Giving all Duplex.			
5 W. H.	8	0	8
13 J. C.	2	0	2
33 T. S.	8	0	8
39 J. P.	6	0	6
41 W. H.	7	0	7
43 G. L.	6	0	6
55 J. B.	10	0	10
57 J. B.	3	0	3
59 C. B.	12	0	12
65 J. F.	7	0	7
69 B. H.	5	0	5
71 R. E.	6	0	6
73 A. S.	6	0	6
81 T. C.	9	0	9
83 J. W.	3	0	3
85 W. P.	4	0	4
103 H. E.	5	0	5
117 C. H.	6	0	6
123 J. S.	4	0	4
129 J. W.	8	0	8
131 J. G.	6	0	6
135 T. W.	4	0	4
139 J. B.	3	0	3
141 M. C.	2	0	2
145 W. P.	2	0	2
161 J. M.	5	0	5
173 B. B.	10	0	10
177 F. S.	2	0	2
191 E. G.	4	0	4
211 T. R.	2	0	2
215 C. W.	3	0	3
223 H. G.	4	0	4
237 G. K.	4	0	4
259 G. G.	3	0	3
265 J. R.	5	0	5
269 W. P.	3	0	3
275 A. P.	8	0	8
37	195	0	195
(*b*) Giving Duplex and Simplex.			
107 W. S.	1	1	2
111 J. W.	2	1	3
115 T. B.	3	1	4
165 E. E.	5	1	6
169 G. B.	5	1	6
219 J. R.	5	1	6
227 E. H.	2	1	3
249 H. H.	6	2	8
253 A. F.	3	2	5
261 J. M.	4	2	6
263 A. N.	3	3	6
267 E. D.	3	1	4
271 W. W.	3	1	4
13	45	18	63

Duplex-Simplex Matings.

The 69 matings of duplex and simplex parents also gave two kinds of results: (*a*) 17 families produced 66 offspring, all of the duplex type; (*b*) 52 families produced 258 offspring, of which 121 were duplex and 137 were simplex.

Table III (*a*) and (*b*) give the numbers found in each family.

Table III.—Duplex × Simplex.

Number and initials of ♂ parent.	Duplex.	Simplex.	Total offspring.
(*a*) Giving all Duplex.			
9 S. E.	2	0	2
45 J. H.	8	0	8
53 D. A.	2	0	2
67 J. H.	9	0	9
77 M. G.	3	0	3
121 L. C.	4	0	4
125 E. R.	3	0	3
143 W. D.	4	0	4
147 W. B.	2	0	2
167 T. C.	7	0	7
181 J. B.	5	0	5
201 E. A.	3	0	3
205 W. B.	4	0	4
209 J. H.	2	0	2
213 J. K.	2	0	2
239 H. C.	3	0	3
245 J. T.	3	0	3
17	66	0	66

Table III—*continued.*

Number and initials of ♂ parent.	Duplex.	Simplex.	Total offspring.
(*b*) Giving Duplex and Simplex.			
1 C. H.	3	2	5
3 G. F.	0	6	6
7 W. E.	3	5	8
17 W. J.	1	1	2
19 F. B.	3	1	4
21 J. B.	4	5	9
23 T. P.	0	4	4
25 R. B.	2	3	5
29 A. F.	5	5	10
35 R. C.	3	4	7
37 S. E.	4	2	6
47 J. S.	3	3	6
49 T. K.	2	2	4
51 G. D.	1	2	3
61 T. C.	5	1	6
63 T. L.	4	5	9
75 J. A.	2	3	5
79 W. W.	4	3	7
87 J. B.	5	4	9
95 J. R.	4	5	9
99 C. C.	5	4	9
109 W. P.	1	1	2
119 J. T.	2	4	6
127 G. S.	3	1	4
149 H. T.	1	4	5
151 W. R.	5	2	7
153 J. M.	3	3	6
155 W. N.	1	1	2
157 T. L.	3	3	6
159 W. H.	4	1	5
163 W. H.	3	3	6
171 D. S.	4	3	7
175 J. C.	2	3	5
179 G. G.	1	1	2
183 W. E.	1	1	2
185 R. S.	2	3	5
187 R. A.	1	1	2
189 G. K.	2	4	6
193 T. C.	1	2	3
195 J. P.	3	1	4
197 J. P.	1	1	2
203 A. P.	1	2	3
207 J. L.	1	1	2
225 C. H.	3	1	4
229 J. N.	1	2	3
233 J. B.	0	4	4
241 J. R.	2	3	5
243 J. F.	2	1	3
247 J. H.	0	2	2
251 A. B.	2	3	5
273 J. P.	2	1	3
279 E. C.	0	4	4
52	121	137	258

With regard to the heredity of the duplex and simplex types, the above tables show that:—

(1) Simplex parents mated together give all simplex offspring.

(2) Duplex parents mated together give either (*a*) all duplex offspring, or (*b*) duplex and simplex offspring in the proportion of about 3 : 1.

(3) Duplex parents mated with simplex parents give either (*a*) all duplex offspring, or (*b*) duplex and simplex offspring in the proportion of about 1 : 1. It is evident, therefore, that the simplex type, in heredity, behaves as a Mendelian recessive to the duplex type, which is dominant. We have already seen that the duplex type differs from the simplex type by the presence of anterior pigment in the iris.

The unit-characters concerned in the heredity of the duplex and simplex types of eyes are, therefore, presence (duplex) and absence (simplex) of anterior pigment in the iris, presence being dominant over absence, which is recessive.

The duplex parents in Tables II (*b*) and III (*b*) are all obviously heterozygous, carrying the simplex character in a recessive state.

The duplex parents in Tables II (*a*) and III (*a*) may be either homozygous or heterozygous.

The duplex parents in Table III (*a*) with large families are almost certainly homozygous, but in those with small families the numbers of offspring are insufficient to test adequately the gametic constitution of the duplex parents. Similarly in the case of the large families in Table II (*a*), one of the duplex parents is almost certainly homozygous, while the other parent may be either homozygous or heterozygous.

In the small families the numbers of offspring are again too small to test adequately the gametic constitution of the duplex parents.

In proof of this we have the fact that in Table III (*a*) each of the three duplex parents of families 53 D. A., 125 E. R., and 209 J. H. is known to have a simplex parent and consequently must be heterozygous, though none of them has yet produced simplex offspring. Similarly in Table II (*a*) both duplex parents of family 13 J. C. are known to have a simplex parent, though they have not yet produced any simplex offspring. As might be expected in a mixed population, some of the simplex parents observed are known to have been extracted from a duplex parent, or to have had duplex brethren.

For instance, in Table I, at least one of the simplex parents of families 15 A. F., 97 H. C., 231 W. K., 255 J. H., and 257 J. C. is known to have a duplex parent, while of the families 31 D. N. and 243 J. F. one parent at least has duplex brethren.

In accordance with the Mendelian principles, the extracted simplex type

breeds true to the simplex character without reversion to its duplex ancestors. In view of recent Mendelian experiments with plants and animals, it did not seem impossible that some simplex individuals at least might be carrying factors which on meeting, in the process of fertilisation, with other complementary factors, might give rise to reversions of the duplex type, but, so far, no such cases have been found. For the present, therefore, while remembering such a possibility, we must take it that the duplex and simplex types of eye-colour in man constitute a simple Mendelian case of presence and absence of a certain pigment.

With regard to the different patterns of duplex eyes and their various shades, my facts, so far, do not enable me to determine positively their genetic relations. The chief difficulty is due to the fact that the anterior pigment present in children tends to increase with age, though to what extent, or to what age, is not yet known, owing to the limited period of observation.

In the few families observed, with all adult offspring, the evidence suggests that the ringed pattern is recessive to the self-coloured pattern, which is dominant; but with regard to the genetic relations of the spotted pattern to the ringed and self-coloured patterns there is practically no evidence available.

Previous Work.

Large numbers of records of eye-colours have been compiled and discussed by anthropologists and biometricians at home and abroad. In most cases, however, the data relate to certain sections of the population, such as school children and conscripts, not analysed or grouped according to their families. So far, I have found only two memoirs which approach the question of the inheritance of eye-colour in man by a comparison of parents with their offspring. The first is that of Alphonse de Candolle.*

De Candolle, with the assistance of some 28 experienced observers, collected a number of records of the inheritance of eye-colours in Switzerland, Germany, and Sweden. De Candolle made two classes of eye-colours, "brown" and "blue," omitting all doubtful shades. The "brown" class included "black," "brown," "yellow-brown," and "green-brown." The "blue" class included "blue," "blue-grey," "grey," "green-blue," and "green-grey." Comparing de Candolle's classes and shades with mine, it is evident that all the "brown" class belong to the duplex type with anterior pigment, but that only part of the "blue" class belong to the simplex type, without anterior pigment.

* "Hérédité de la Couleur des Yeux dans l'Espèce Humaine," 'Archives des Sciences, Genève (3ème période, vol. 12, 1884, pp. 97—119).

The second memoir is that of Mr. Francis Galton.* Mr. Galton collected a number of records of family eye-colours in the British Isles, among the "Records of Family Faculties"—known as the R.F.F. data. These family records were obtained through the offer of prizes to the public.†

From the family records sent in, Mr. Galton made three classes of eye-colours, "light," "hazel," and "dark." The "light" class included the shades recorded as "light blue," "blue," "dark blue," "grey," and "blue-green." The "hazel" class included "dark grey" and "hazel." The "dark" class included "black," "very dark brown," "dark brown," "brown," and "light brown." Comparing the shades of colour sent in to Mr. Galton by his correspondents with mine, it is evident that all of Mr. Galton's "dark" class belong to the duplex type with anterior pigment. With regard to the "hazel" class, part of these would probably represent my ringed duplex pattern, while the remainder might belong either to the duplex or simplex type, according to the interpretations of the colours by different observers. Mr. Galton apparently regards "dark grey" and "hazel" as bicolour eyes,‡ which would make them practically equivalent to my ringed duplex eyes. In view, however, of my experience with popular descriptions of eye-colours, it is highly probable that many of Mr. Galton's correspondents would record certain forms of self-coloured duplex eyes as "hazel," and certain forms of "simplex" eyes as "dark grey." Mr. Galton's "light" class would apparently consist partly of the simplex type without anterior pigment, and partly of the low-grade forms of the duplex type with some anterior pigment. In the nature of the circumstances in which the R.F.F. data were recorded, it cannot, of course, be expected that the observations were critical in regard to the presence or absence of anterior pigment in the iris. On the whole, therefore, it does not seem possible to express either de Candolle's or Mr. Galton's classes and shades of eye-colours in terms of duplex and simplex pigmentation. It was on Mr. Galton's R.F.F. data that Professor Karl Pearson based his memoir "On the Inheritance of Eye-colour in Man,"§ and afterwards concluded that nothing corresponding to Mendel's principles appeared in the characters for eye-colour in man.‖

* "Family Likeness in Eye-colour," 'Roy. Soc. Proc.,' 1886, vol. 40, No. 245, pp. 402—416.

† See 'Natural Inheritance,' 1889, pp. 72—78.

‡ *Loc. cit.*, pp. 142, 144.

§ 'Phil. Trans.,' A, 1900, vol. 195, p. 102.

‖ 'Biometrika,' 1903, vol. 2, pp. 213, 214.

Summary.

An examination of the eye-colours of a number of parents and their offspring in a Leicestershire village shows that there are at least two discontinuous types of iris in man:—

(1) The duplex type, with both anterior and posterior pigments, as in ordinary brown eyes.

(2) The simplex type, with posterior pigment only, the anterior pigment being absent, as in clear blue eyes.

In heredity the simplex type behaves as a Mendelian recessive to the duplex type, which is dominant. The unit characters concerned are evidently presence (duplex) and absence (simplex) of anterior pigment on a basis of posterior pigment, presence being dominant.

The duplex and simplex types can be distinguished at any age. Various pigmental and structural changes take place in the iris during childhood and youth, the extent of which is not yet known. Few families with living parents and offspring, all adult, are to be found in one village. Consequently, it has not yet been possible to determine the genetic relations between the various shades of the duplex type.

Note.—I desire to acknowledge my indebtedness to Mr. W. Bateson for some valuable criticisms and suggestions in regard to the preparation of this paper, and also to Mr. R. C. Punnett, who came down and examined a number of the simplex eyes recorded above.

(*Note added* 11*th January*, 1908.)

Since the above paper was presented, an article on "Heredity of Eye-colour in Man" has appeared in 'Science,' 1907, vol. 26, pp. 589—592 (dated 1st November), in which Professor C. B. Davenport independently arrives at similar conclusions, pointing out the Mendelian inheritance of eye-colour in man.